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INTRASPECIFIC GROUPINGS IN GONATID SQUIDS

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ABSTRACT. In the tows from epipelagic layer (0-50 m) in the southern part of the Okhotsk Sea and in the NW Pacific off Kurile Islands (118 one-hour trawling by large-sized midwater otter-trawls) and mesopelagic (500-300-200 m) layers up to 200 nautical miles east-southeastward off Southern Kuriles (11 tows) in July-August, 1992, the squid *Gonatopsis borealis* occupied 1-2nd places by abundance and biomass among all squids and was represented by two groupings, small sized early-maturing (SG) and large sized lately-maturing (LG). SG was distributed through the entire area investigated and LG — only to the south and southeast of Southern Kuriles. Modal dorsal mantle length (DML) in mature males and maturing females of SG was 12-17 and 13-17 cm, of LG — 20-26 and 22-27 cm. In the epipelagic layer of the Okhotsk Sea, the maturing squids were rare, mature absent in catches; in the NW Pacific mature males and maturing females were found in both epipelagic and mesopelagic layers, but none mature mated female was caught. The growth of penis in males began at DML 10-11 cm (transition from I to II stage of maturity) and strongly slowed down at DML 19-20 cm. LG males were represented by fully mature individuals only, immature males could not be divided into SG and LG. The growth of nidamental glands in females proceeds with acceleration and almost parallel in both SG and LG groups. There were some uncommon females with DML typical for SG but with nidamental gland length less than in most SG females. They were supposedly LG females. If so, the difference between SG and LG females is determined much earlier than they mature. The gonadosomatic index (gonad weight/total weight) in LG males was somewhat higher than in SG, while in LG females it was less than in SG at the same stage of maturity. The Commander squid *Berryteuthis magister* was found to be unusually rare in both the Okhotsk Sea and the NW Pacific: 0.16 and 0.04% of all squid biomass respectively. Except isolated specimens of usual size range, off Eastern Sakhalin there were caught two males at II and III stages and four females at II stage of maturity of unusually small size, DML 6-10 cm (as a rule, the transition from I to II stage occurs at DML 14-18 cm). It is possible that they belonged to a previously unknown early-maturing grouping which may appear only in times of strong decline of the abundance of common grouping. The status of SG and LG in gonatids is discussed in comparison with that in loliginids and ommastrephids.

Key words: squids, Gonatopsis borealis, Berryteuthis magister, *distribution, maturation, intraspecific groupings, Okhotsk Sea, Northwest Pacific.*

Introduction

The phenomenon of intraspecific groupings is well known for commercially most important squid families — ommastrephids and loliginids (Nesis 1977, 1985). It was noted also for sepiid cuttlefishes and octopodid octopuses. It consists in the existence of two or more groupings of individuals within the same species differing in the place and/or time of spawing and/or foraging, in the growth rate and size at maturity. This phenomenon is perfectly analogous to the long known phenomenon of intraspecific groups in fishes (landlocked and anadromous forms, seasonal races in anadromous fishes and cyclostomes: e.g. Berg 1934, Nikolsky 1965, etc.). The intraspecific groupings in squids are very diverse and species-specific but it is possible to recognize two main types.

In the neritic (family Loliginidae) and nerito-oceanic (family Ommastrephidae, subfamilies Illicinae and Todarodinae) squids there are two to four seasonal groupings with different time and (commonly but not obligatorily) places of spawning, different migration distances and areas of foraging; the maturity sizes are, as a rule, also different but not greatly, while the duration of life is approximately the same. Such groupings are known, for example, in *Loligo edulis, L.*

patagonica, Illex illecebrosus, I. argentinus, Todarodes sagittatus, T. pacificus, Nototodarus sloani, N. gouldii (Arkhipkin 1990, Brunetti 1990, Froerman 1985, Hatanaka et al. 1985, Hatfield 1992, Kawakami 1976, Mangold 1987, Mattlin et al. 1985, Murata 1990, Natsukari et al. 1988, Nigmatullin 1989, O'Dor 1992, Okutani 1983, Patterson 1988, Shevtsov 1978, Shimko 1984, Wiborg et al. 1982, etc.).

In the oceanic and transitional between nerito-oceanic and oceanic squids (family Ommastrephidae, subfamily Ommastrephinae) there are commonly two or three entirely or partially sympatric groupings that may differ in the places and time of spawning, in foraging areas, and, what is most important, in the size at maturation which may twofold differ; these groupings differ also in the life span but not as greatly as in the size. Such groupings are known in *Dosidicus gigas, Ommastrephes bartramii, Sthenoteuthis pteropus, S. oualaniensis* (Murakami et al. 1981, Murata 1990, Nesis 1983, 1993, Zuev 1975, Zuev et al. 1985, etc.).

The problem of taxonomic rank of these groupings is open to discussion (see Zuev et al. 1985). The attempts to evaluate their status by the genetic-biochemical methods yielded ambiguous results: all possibilities from absence of genetic differences (Natsukari et al. 1986 for *Loligo edulis*, Carvalho and Pitcher 1989 for *L. patagonica*) to differences of full species rank (Carvalho et al. 1992 and Tsygankov 1988 for *Illex argentinus*) have been found. As a rule it is stated that they are different stock units, i.e. have interpopulational rank (Nesis 1993). In gonatids (family Gonatidae), the intraspecific groupings are as yet known for only one species: *Gonatopsis borealis*, the Boreopacific gonate squid. They were discovered by Naito et al. (1977 a, b) and studied by Kubodera et al. (1983). According to these data there are two size groups in *G. borealis*, small-sized (early-maturing) and large-sized (lately-maturing). By the summer the size of squids of both groups almost do not overlap: males and females of the first group have dorsal mantle length (DML) less than 18 cm, of the other — more than 19-20 cm. Both groups occur in the northern North Pacific but large squids are distributed in more southern and eastern areas than the small ones and their ranges are hardly overlapped (Kubodera et al. 1983, Naito et al. 1977 a, b). The Japanese authors think that they are two geographically separated subpopulations, each with a distinct size composition and independent development of reproductive organs. However it is unclear if they have the same life cycle and live only one year (Naito et al. 1977b) or belong to different age groups of the same population (the large squids may be individuals of small size group, which have no time to mature together with most part of their coevals and survive the second winter), or, at last, they are completely separate populations with different biological characteristics (Kubodera et al. 1983, pp. 36, 45). Recently (Nesis 1989) specimens of larger squids were found, though in very small quantities, in the Okhotsk Sea too, thus the area of range overlap was considerably enlarged, and it was suggested (Nesis 1989, p. 55) that there are two suprapopulational groupings and that small size squids may live for one, while large size — two years.

During the summer 1992 the senior author had a possibility to collect additional data on intraspecific groupings of gonatids in the Okhotsk Sea and Northwest Pacific Ocean off Kurile Islands.

Material and methods

The material was collected in the cruise of the fishery reconnaissance vessel (a converted super-trawler) «Novoulyanovsk» in southern part of the Okhotsk Sea (southward of the line connecting the coast of central-eastern Sakhalin at 51°N with Diane Strait at 47°30′N) and in the Northwest Pacific off middle and southern part of Kurile Island chain up to 200 nautical miles (NM) from the coast, July 14th to August 17th, 1992. 118 one-hour trawlings were made in the epipelagic layer in the day- and night-time with large midwater trawls RT 118/620 (35 tows) and RT 93/500 (83 tows). The vertical opening of the first trawl was 50 m, the horizontal one was 80 m; those of the second trawl were 45 and 50 m respectively. Trawlings were made at the speed of 4.5-5.5, usually 5.0 knots in such a way that the screens of headrope went at the very surface. Under this condition the trawl catches the layer between the surface and the depth of 50 m (first trawl) or 45 m (second trawl).

Besides the epipelagic tows there were made 11 mesopelagic trawlings with the trawl RT 93/500. They were made in the NW Pacific Ocean approximately up to 100 and 200 NM eastward and southeastward of Southern Kurile Islands. Trawlings were performed stepwise at horizons of 500, 300 and 200 m; at each depth the trawl went for the same time, 20 min on the average. Trawlings were made at the speed of 3.0-4.5 knots, catches were recalculated to one hour of trawling at the speed of 3.0 knots. All mesopelagic trawlings were made at the same stations as epipelagic ones.

Caught squids were identified, measured and weighted. In the females the signs of mating were noted. In *G. borealis* spermatophores are implanted on the buccal membrane, in *Berryteuthis magister* — on inner mantle side in mantle cavity, near gill bases. Maturity stages were identified in dissected specimens according to Nigmatullin's (1989) maturity scale of 7 stages, from 0 (sex indeterminable) to VI — spent; stage V (mature animals) subdivided into three substages. Stomach filling was determined on the five-stage scale (Zuev et al. 1985). The nidamental gland and penis length were measured, the reproductive system was weighted. Weight of reproductive system was determined only in large squids at advanced maturity stages because the weighting of small specimens on swinging ship is difficult: the error is too great. The food composition in stomachs was visually identified. In the present paper only the data are given on sizes and maturity of squids and their relationship.

In overall 1746 *G. borealis* and 57 *B. magister* were measured, 471 and 28 respectively were dissected. The small and evidently immature specimens were not dissected. Data on size structure and maturity stages of squids were analyzed using standard methods of mathematical statistics. All calculations were made on IBM PC/AT computer with the SYSTAT version 5.0 software package.

Three parameters of size structure were analyzed: dorsal mantle length (DML), penis length (PL) in males and nidamental gland length (NGL) in females. The relationships between PL, NGL and DML were calculated. For each maturity stage, the indexes were calculated as follows: the mean, standard deviation, minimal and maximal values and significance of differences between the averages for different stages. To do this the Tuckey method of multiple comparisons was used. All calculations were made by the junior author.

Results

The Boreopacific gonate squid, Gonatopsis borealis

G. borealis occupies the first place in abundance (68.2% of all squids) in the catches in the Okhotsk Sea, and the second place in the Pacific Ocean after very common small firefly squid *Watasenia scintillans* (28.8%); by the weight it ranks second in both areas after Japanese flying squid *Todarodes pacificus* (35.4% in the Okhotsk Sea, 35.9% in the NW Pacific). If we assume, according to TINRO methodology, that the trawl catchability for squids is 0.1, the total abundance of *G. borealis* over the entire area studied is 3.9 billion specimens and the total biomass of 87 thousand tons.

G. borealis was recorded throughout the area studied except shallow-water areas off Southern and Eastern Sakhalin and South Kurile Shallows (Fig. 1). High abundance was recorded in both the Okhotsk Sea and the NW Pacific but in the Okhotsk Sea the catches were no more than 15 kg/h while in the Pacific they were sometimes much higher, up to 150 kg/h southeastward of northern Kunashir Island.

The squids were caught in both epipelagic and mesopelagic layers. Seaward of Southern Kuriles, the total biomass of *G. borealis* in mesopelagic layers (average for 200 to 500 m layer) was found to be the same as in the epipelagic (0-50 m) layer, 31.1 and 31.2 thousand tons respectively.

The size structure of squids was very different in the Okhotsk Sea and NW Pacific (Fig. 2a). In the Okhotsk Sea, the young individuals predom-

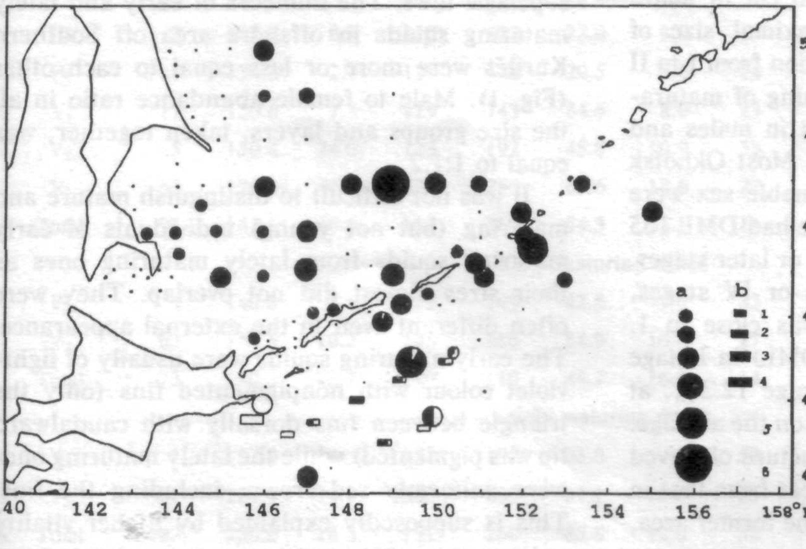

Fig. 1. Distribution of *Gonatopsis borealis* in epipelagic (a) and mesopelagic (b) layers of the Okhotsk Sea and NW Pacific off Kurile Islands, July 14th — August 17th, 1992. 1 — 1-25, 2 — 26-100, 3 — 101-500, 4 — 501-1000, 5 — 1001-2000, 6 — >2000, specimens per trawling hour. Sectors represent the portions of squids of lately maturing (white) and early maturing (black) group. The number of specimens in catches was counted for squids of all sizes, the portions of early and lately maturing groups — only for squids at advanced stages of maturity.

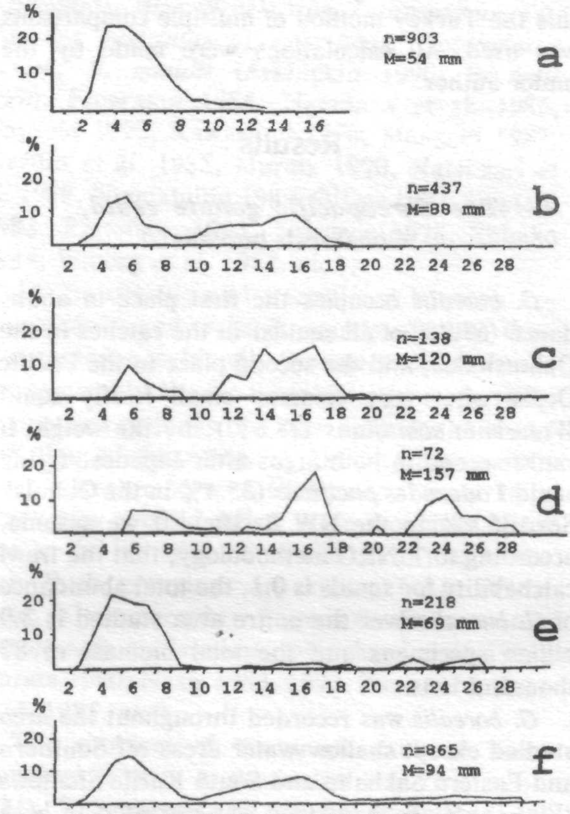

Fig. 2. Size distribution in *Gonatopsis borealis*. a — Okhotsk Sea, total, b — Middle Kuriles, c-e — Southern Kuriles: nearshore zone (c), offshore zone, epipelagic layer (d), the same, mesopelagic layers (e), f — NW Pacific, total.

inated in the epipelagic layer. The size distribution was unimodal, the average size was 5.4 cm, the modal group (DML 3-6 cm) included two thirds of all squids. In different parts of the area studied the size structure was rather similar. The average DML in the Okhotsk Sea varied from 4.8 cm off Middle Kuriles (Simushir — Urup Islands) to 6.6 cm off Southern Kuriles (Iturup — Kunashir Islands). Sex may be visually determined beginning from DML 7-10 cm in males and 9.5-10 cm in females. Maximal size of juveniles was 10-12.5 cm. Transition from I to II stage of maturity, i.e. the beginning of maturation, occurred at DML 10-11 cm in males and approximately 12 cm in females. Most Okhotsk Sea squids with visually determinable sex were at I to II stage. The largest female had DML 135 mm. There were no females at III or later stages. There were several males at III or IV stages, DML 111-121 mm. Sex ratio was close to 1. Nidamental gland index (NGL/DML) in I stage females was 9-15%, on the average 12.3%, at I-II and II stages 13-24%, 16.5% on the average.

The pattern of population structure observed in the Pacific is completely different from that in the Okhotsk Sea (Fig. 2 b-f). In the former area, on the north of the area studied, the size distribution becomes bimodal (Fig. 2 b,c), and on the south — trimodal (Fig. 2 d,e). This is caused, firstly, by the appearance of mature males and almost mature females in the NW Pacific and, secondly, by the fact that at the same stations the males and females were caught which were at the same maturity stages but of very different size.

Off the Pacific side of Middle Kuriles at 45-48°N and in the nearshore zone off Southern Kuriles (Iturup and Kunashir Islands) only squids of the small-sized group were recorded (Fig. 2 b,c). Here the juveniles absolutely predominated as well: squids with DML 2 to 6 cm comprised almost 75% of all squids and the modal size group (3-5 cm) constituted more than half of the stock. Predominating male size was 11-15 cm off Middle Kuriles and 13-16 cm off Southern Kuriles (nearshore zone); females were mostly 13-16 cm long in both areas. Male to female abundance ratio was 1:1.55. The most part (75%) of males were fully mature but there were no mature or even maturing females.

The most complex pattern of size structure was found in the offshore zone southeastward of Southern Kuriles at 41°30′— 44°N (Fig. 2 d,e). Here three different size groups of squids separated by clear hiatuses were found: juveniles, DML 2 to 9 cm, mode 3-6 cm; maturing and mature males and maturing females of early-maturing grouping, DML 11-17 cm; mature males and maturing females of lately-maturing grouping, DML 20-28 cm. Squids of all three size groups were caught in both epipelagic and mesopelagic layers but mature and maturing animals of two larger groups were more common in epipelagic tows while juveniles — in mesopelagic ones. As a result, the average DML in epipelagic tows was more than twice larger than in mesopelagic tows. The numbers of early and lately maturing squids in offshore area off Southern Kuriles were more or less equal to each other (Fig. 1). Male to female abundance ratio in all the size groups and layers, taken together, was equal to 1:1.2.

It was not difficult to distinguish mature and maturing (but not young) individuals of early maturing squids from lately maturing ones as their sizes almost did not overlap. They were often different even in the external appearance. The early maturing squids were usually of light-violet colour with nonpigmented fins (only the triangle between fins dorsally with caudalward tip was pigmented) while the lately maturing ones were uniformly red-brown, including the fins. This is supposedly explained by higher vitality of large squids which arrive on board usually alive, and/or by greater thickness (or greater firmness) of their skin, particularly the skin of fins which, as a rule, is thin and easily striped. Mantle skin, including triangle between fins, in *G. borealis* is usually firm but in juveniles and in adult squids of the small-sized group it is easily separable from the mantle muscles and peels off as a stocking while in adults of the large-sized group it adheres tightly to underlying tissues.

The size of males of the NW Pacific early maturing squids at III, IV and V stages of maturity were 110-123, 123-128 and 119-169 (?180) mm respectively, at substage V_3 — 126-169 (?180) mm (Table 1). Relative penis length increased from 14-26% in III stage males to 21-57% in V_3 males (Table 1). Gonadosomatic index (gonad weight/total weight) increased only slightly with growth: from 0.8-1.7%, on the average 1.1%, in III stage males to 0.9-3.6%, on the average 1.8%, in V_3 stage males. This is characteristic of the maturation process in squid males as the increase in size and weight of spermatophoric organ complex, including the mass of spermatophores, proceeds parallels to exhaustion of the mass of testis.

All early maturing males caught offshore off Southern Kuriles were mature (V_1-V_3), their size — 13-17 (?18) cm — was the same as in near-shore zone off Southern Kuriles and off Middle Kuriles. Relative penis length was also the same as well as gonadosomatic index (PL/DML off Southern Kuriles at V_3 substage is 34-44, on the average 38.9%, mean gonadosomatic index 1.4%). Lately maturing males were also mature. Their sizes were (?18) 19-26 cm, on the average 22,8 cm; if excluding the male with DML 180 mm at V_3 substage, which may be either unusually large specimen of the small-sized group or unusually small one of the large-sized group, the average DML in large males was 23.0 cm, i.e. more than half as much as in small-sized males.

Statistical processing of data on all males of III to V stages (93 from the NW Pacific and 1 from the Okhotsk Sea) whose penis length was measured, shows that by average DML only V_3 substage significantly (at 95% level) differs from all other stages except V_2; the other stages differ insignificantly. By the PL/DML ratio, the males IV are significantly different from all substages of V stage but not from III stage; substages V_1 and V_3 also significantly differ from each other.

In the group of early maturing males, the substage V_3 differs significantly by DML from III, IV and V_1 and the stage III is significantly different from IV. By PL/DML ratio, the males IV are different from all substages of V stage and the V_3 substage — from III, IV and V_1. Of 22 lately maturing males only one was at the V_2 substage (DML 192 mm), all other were fully mature, V_3, DML 205-260, on the average 231.9 mm (Table 1).

The penis growth in early maturing males at II to V stages proceeds almost linearly and practically with the same rate as the mantle growth (Fig. 3). In large-sized males, the fore-end of penis reaches the anterior mantle margin, then its further growth becomes useless, all the

Table 1. Number of squids measured (n), average (m), standard deviation (s), minimum and maximum values of the dorsal mantle length (DML) and penis length (PL), mm, in males of *Gonatopsis borealis* at different stages of maturity.

Stage of maturity	n	DML				PL				PL/ML			
		m	s	Min	Max	m	s	Min	Max	m	s	Min	Max
						All males							
III	3	117.3	6.7	110	123	22.0	8.9	15	32	0.18	0.07	0.14	0.26
IV	5	124.3	2.7	121	128	20.5	5.6	14	30	0.16	0.05	0.11	0.25
V_1	17	130.6	7.3	119	143	34.5	8.9	23	58	0.26	0.06	0.18	0.24
V_2	5	150.4	24.0	133	192	45.8	10.9	33	58	0.30	0.05	0.24	0.38
V_3	63	176.4	41.2	126	260	65.6	18.6	27	105	0.37	0.05	0.21	0.57
Total	95	161.1	40.6	110	260	54.3	23.1	14	105	0.33	0.09	0.11	0.57
						Early maturing males							
V_2	4	140.0	7.1	133	149	42.8	9.6	33	56	0.30	0.06	0.24	0.38
V_3	63	148.6	10.2	126	180	54.9	10.6	27	90	0.37	0.06	0.21	0.57
Total	73	140.3	13.7	110	180	44.7	16.0	14	90	0.31	0.09	0.11	0.57
						Lately maturing males							
V_2	1	192.0	—	192	192	58.0	—	58	58	0.30	—	0.30	0.30
V_3	21	231.9	14.1	205	260	87.1	10.5	65	105	0.38	0.04	0.30	0.48
Total	22	230.0	16.2	192	260	85.8	12.0	58	105	0.37	0.04	0.30	0.48

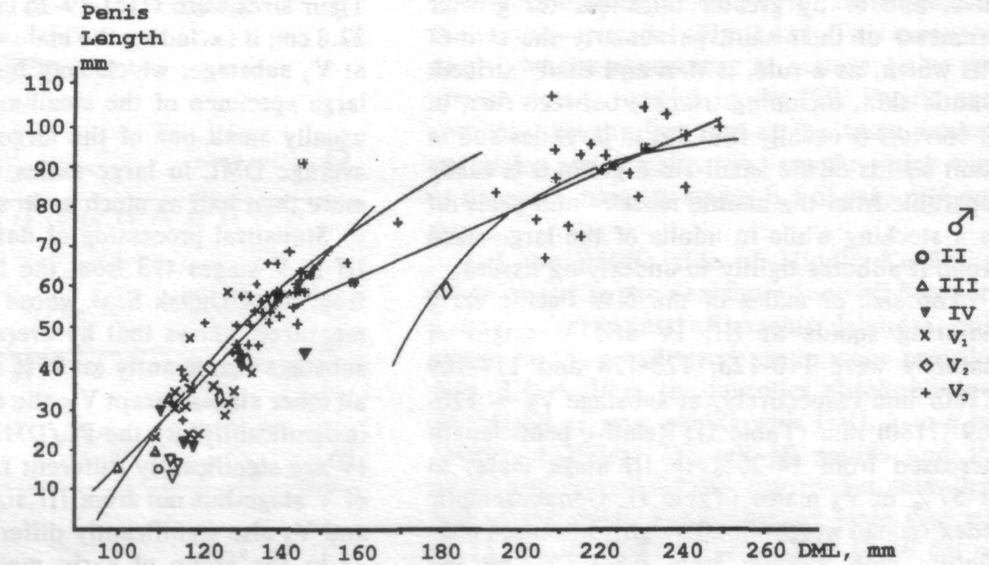

Fig. 3. Penis length to dorsal mantle length (DML) ratio in males of *Gonatopsis borealis* at II to V_3 stages of maturity. The lines are shown of linear and non-linear regression, their coefficients are given in the text.

more the penis is well dilatable. In mature lately-maturing males the penis length is highly variable and ranges from 20 to 26 cm. The penis growth proceeds at much lower rate than that of the mantle. Relative penis length in these males is 30-48%, on the average 37.4%, which is almost the same as in mature early maturing males.

The linear regression equations of the penis growth are as follows:
for early maturing males

$$PL = -98.10 + 1.02\ DML,\ r = 0.867;$$

for lately maturing males

$$PL = -13.04 + 0.43\ DML,\ r = 0.580.$$

Both coefficients in the equation for early maturing males are significantly different from zero at highest significance level but the coefficient of slope is no different from 1. In lately maturing males only the coefficient of slope (0.43) is significantly different from zero while the constant (-13.04) is not. Coefficients of slope in both equations are significantly different from each other (Student's t-criterion is 3.867).

The von Bertalanffy-like equation gives somewhat better approximation than the linear one:

$$PL = PL_\infty\ (1 - \exp\ (-K\ (DML - DML_0))),$$

where PL_∞ is the penis length at maximum possible DML, DML_0 is the size at which the penis begins to grow, K — coefficient. The parameters of computed equations are as follows: for early maturing males:

$PL_\infty = 134.8 \pm 22.6;$
$K = 0.012 \pm 0.003;$
$DML_0 = 104.2 \pm 2.4;$

for lately maturing males

$PL_\infty = 97.1 \pm 9.96;$
$K = 0.035 \pm 0.024;$
$DML_0 = 164.6 \pm 19.3.$

Differences between PL_∞ and K for both groups are insignificant by t-criterion but these between values of DML_0 are significant (for PL_∞ $t = 1.52$, $0.05 < p < 0.1$; for K $t = 0.95$, $p < 0.15$; for DML_0 $t = 8.44$, $p < 0.005$).

The line of regression for early maturing males crosses the X-axis at DML approximately 10-11 cm that equals the size at the beginning of maturation, i.e. the transition from I to II stage of maturity. At DML approximately 19-20 cm, the regression lines of the penis length level off and the relative penis length remains at level close to 37% DML.

Gonadosomatic index in lately maturing males is somewhat higher than in early maturing ones: 1.6-2.9% at V_3 substage, on the average 2.0%, against 1.4-1.8% in early maturing males.

The most mature females of early maturing group in the NW Pacific were at transitional III-IV stage of maturity, the transition of mature oocytes from the ovary into the oviduct did not yet begin. Size of females at III stage was 131-173 mm, at III-IV stage 146-173 mm (Table 2). One female at III stage with DML 188 mm occupied a transitional position between early and lately maturing groups (see below). Average nidamental gland index (NGL/DML) in III and III-IV stage females was 23.4 and 26.7% respectively. Gonadosomatic index increased in the course of maturation at much higher rate than in males. At I, II, III and III-IV stages it was 1.0, 1.4, 3.2 and 12.5% respectively (data were available for only one III-IV stage female).

Offshore of Southern Kuriles, the females of both groups were at various stages of maturity, from I-II to III-IV, the majority at III and III-IV. No mature mated female was caught in both epipelagic and mesopelagic tows. This may mean that females mature, mate and spawn in deep bathypelagic layers.

The size of early maturing females in offshore zone seaward of Southern Kuriles, as well as that of males, was no different from their size in coastal zone off Southern Kuriles and off Middle Kuriles: at III stage the DML was 150-170, on the average 157.4 mm, and at III-IV stage — 152-173, on the average 162.5 mm. Average nidamental gland index was 27.5 and 33.8% respectively, the mean gonadosomatic index — 6.4 and 10.3%. Lately maturing females were, like the males, more than half as much as early maturing ones at the same stages of maturity. Their DML at III stage was 223-274, on the average 247.6 mm, at III-IV stage — 247-272, on the average 259.5 mm. Nidamental gland index was 18-29, on the average 25.7%, and 29-31, on the average 30.3%, respectively (Table 2). Gonadosomatic index in III stage females was 1.4-4.0, on the average 2.7%, in one III-IV stage female 3.8%.

By the size (DML) the females at I stage (all areas together) were significantly different from females at II and subsequent stages except for those at transitional I-II stage; the latter and the stage II females were different from stage III and

Table 2. *Number of squids measured (n), average (m), standard deviation (s), minimum and maximum values of the dorsal mantle length (DML) and nidamental gland length (NGL), mm, in females of Gonatopsis borealis at different stages of maturity.*

Stage of maturity	n	DML				NGL				NGL/ML			
		m	s	Min	Max	m	s	Min	Max	m	s	Min	Max
						All females							
I	30	112.7	10.6	95	135	13.8	3.2	7	22	0.12	0.02	0.06	0.17
I-II	8	130.5	16.1	118	168	18.9	2.1	17	22	0.14	0.01	0.13	0.16
II	48	135.6	22.1	108	240	21.8	5.6	13	43	0.16	0.02	0.10	0.24
II-III	9	165.7	34.5	131	230	34.8	10.3	22	56	0.21	0.04	0.16	0.25
III	59	180.4	42.7	131	274	45.2	13.3	22	77	0.25	0.04	0.15	0.33
III-IV	8	183.0	48.6	146	272	54.1	16.6	37	80	0.29	0.03	0.25	0.34
Total	162	151.4	41.7	95	274	31.0	16.8	7	80	0.19	0.06	0.06	0.34
						Early maturing females							
I	29	112.2	10.5	95	135	13.9	3.3	7	22	0.15	0.01	0.13	0.16
I-II	7	125.1	5.8	118	135	18.4	1.8	17	21	0.15	0.01	0.13	0.16
II	45	131.5	11.1	108	158	21.2	4.3	13	32	0.16	0.02	0.11	0.24
II-III	7	149.0	10.9	131	165	31.4	7.2	22	41	0.21	0.04	0.16	0.25
III	42	154.7	8.7	131	173	38.5	6.7	22	53	0.25	0.04	0.15	0.33
III-IV	6	157.5	10.8	146	173	46.0	8.2	37	58	0.29	0.04	0.25	0.34
Total	136	136.7	19.2	95	173	26.5	11.7	7	58	0.19	0.06	0.06	0.34
						Lately maturing females							
I	1*	127.0	—	127	127	12.0	—	12	12	0.09	—	0.09	0.09
I-II	1*	168.0	—	168	168	22.0	—	22	22	0.13	—	0.13	0.13
II	3*	196.7	53.4	137	240	30.0	14.7	14	43	0.14	0.04	0.10	0.18
II-III	2	224.0	8.5	218	230	46.5	13.4	37	56	0.21	0.05	0.17	0.24
III	17	244.1	19.6	188	274	61.8	10.9	35	77	0.25	0.03	0.18	0.29
III-IV	2	259.5	17.7	247	272	78.5	2.1	77	80	0.30	0.01	0.29	0.31
Total	26	230.8	37.5	127	274	54.8	19.3	12	80	0.23	0.06	0.09	0.31

*The belonging of females at I and II stages with DML less than 19 cm to lately maturing group is doubtful.

III-IV females. By absolute values of nidamental gland length all main stages significantly differed from each other, but each main stage insignificantly differed from succesive transitional one, i.e. I from I-II, II from II-III, III from III-IV. By nidamental gland index, only I-II stage females were insignificantly different from both I and II stage females, all other differences were significant. Size differences between early maturing females from the Okhotsk Sea and from NW Pacific were insignificant.

Nidamental gland index in early and lately maturing females at the same stage of maturity was nearly the same (Table 2). Nidamental glands grew with acceleration and almost parallel in both size groups, in spite of 60% difference in DML between small- and large-sized specimens (Fig. 4).

The linear regression equations of the nidamental gland growth are as follows:
for early maturing females

$$NGL = -48.14 + 0.55\ DML,\ r = 0.899;$$

for lately maturing females

$$NGL = -53.08 + 0.47\ DML,\ r = 0.906.$$

Coefficients of regression in both equations are significantly different from zero but insignificantly — from each other ($t = 1.611$, $0.05 < p < 0.1$). Constants (intercepts) of both equations are also insignificantly different ($t = 0.454$).

The power equation, usual for allometric growth, gives somewhat better approximation than the linear one (Fig. 4). F-criterion value for early maturing females is 564.7 for the linear approximation, 750.3 for the power one; 110.3 and 258.7 for lately maturing females respectively.

The power function equations are as follows:
for early maturing females

$$NGL = 0.0000162\ DML^{2.896},$$

for lately maturing females

$$NGL = 0.0000672\ DML^{2.491}.$$

Standard errors for ln *a* are 0.519 and 0.841 for early and lately maturing females respectively, the errors for *b* — 0.106 and 0.155 respectively. Difference between logarithms of *a* in both equations is insignificant ($t = 1.44$, $0.05 < p < 0.1$), but that between power coefficients *b* is significant ($t = 2.16$, $0.01 < p < 0.025$).

As to gonadosomatic index, it is impossible to make a reliable conclusion because of scantity of data. However it is likely that in lately maturing females the index is less than in early maturing ones at the same stage of maturity, i.e. the weight of reproductive system is characterized by a negative allometry. The same follows from data presented by T.Kubodera et al. (1983).

Nidamental gland length in lately maturing females at II, III and III-IV stages up to DML of approximately 20 cm is smaller than in early maturing females at the same stages (see Fig. 4). Taking as a basis the nidamental gland length only (gonadosomatic index, as stated above, is unsuitable for such comparison) and considering, conditionally to some extent, that all females with DML intermediate between small- and large-sized groups (13-19 cm) with small nidamental glands are lately maturing (Table 2), it is possible to distinguish early and lately maturing females at rather early stages of maturation.

For example, most I stage females with DML 10-11 cm have nidamental glands 10-15 mm long, but some — only 7 mm; most stage II females, DML 13-14 cm, have NGL 18-25 mm, while some — only 13-15 mm; most III stage females, DML 16-17 cm, have NGL 38-50 mm, but some — 22 mm. We suppose that females with smaller NGL are lately maturing. Beginning from DML 18 cm, the sizes of early and lately maturing females as well as their nidamental gland length are no longer overlapped. In most early maturing females at III and III-IV stages, NGL is 30-50 mm, in most lately maturing — 50-80 mm. Thus the growth of nidamental glands is related to the female reproductive state rather than to its absolute size. It is incorrect to characterize the changes of female reproductive state by the nidamental gland length only, as it is done rather frequently: this character is important only in comparison with DML and the stage of maturity.

Commander squid,
Berryteuthis magister

In *B.magister* the intraspecific groupings were unknown. By biological characteristics, including such as the egg size, *B.magister* from the Japan Sea is different from any other population of this species due to geographical isolation of the Japan Sea group of populations. In the Japan Sea adult *B.magister* lives at depths more than 200-300 m, thus the shallows of Tatar Strait and Tsugaru Strait are impassable barriers for adult squids (Naito et al. 1977a, Nesis 1989). Squids from the

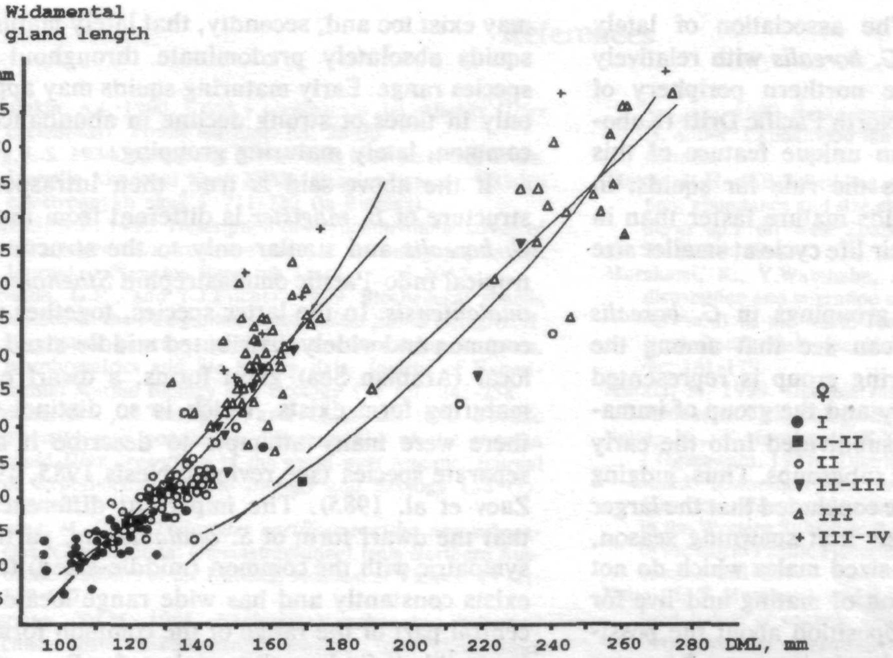

Fig. 4. Nidamental gland length to dorsal mantle length (DML) ratio in females of *Gonatopsis borealis* at I to III-IV stages of maturity. The lines are shown of linear and power regression, their coefficients are given in the text.

Okhotsk and Bering Seas and northern North Pacific off Kamchatka, Commander and Kurile Islands belong to a common stock by biometric data (Nesis 1989).

By genetic-biochemical characters there were distinguished the Kurile, Olyutoro-Navarin and Pribilof-Alaska groups (Katugin 1988, Kovalev 1990); their distinctions are probably caused by the spatial constraint to gene flow (the gene flow in this species is maintained by the drift with current of pelagic paralarvae inhabiting upper water layers).

In the area of our investigations in 1992, both in the Okhotsk Sea and NW Pacific, the abundance of *B.magister* was unusually low. Assuming the catchability coefficient 0.1, the total biomass was slightly more than 40 tons in the Okhotsk Sea and less than 80 tons in the NW Pacific, i.e. 0.16% and less than 0.04% of the total biomass of all squids. Most specimens, as it commonly is in epipelagic tows, were juveniles. Only two specimens larger than 13 cm were caught: a I stage male (DML 145 mm) in the Okhotsk Sea and a III-IV stage female (DML 218 mm) in the NW Pacific. Size of both fell within the limits usual for squids at these stages of maturity (Naito et al. 1977b, Nesis 1989).

However off Eastern Sakhalin over the depths of 92 to 320 m, six small specimens of *B.magister* were caught at unexpectedly advanced stages of maturity: two males, DML 80 and 85 mm, at II and III stages and four females, DML 62-99 mm, at II stage. Usually, the transition from I to II stage of maturity in the Okhotsk Sea *B.magister* occurs at DML 14-18 cm, or at twice larger size. The beginning of maturation at such small size as 6-10 cm was reported only in *Berryteuthis anonychus* out of all Gonatidae (V.D.Didenko, pers. commun.). This squid is distributed in the northeastern Pacific and has never been recorded in the Far Eastern seas (Nesis 1985). Nowhere eastward of Sakhalin similar squids were caught.

Discussion

Gonatopsis borealis. Our data confirm the results obtained by Japanese authors (Kubodera et al. 1983, Naito et al. 1977 a,b): *G. borealis* is in fact represented in the northern North Pacific by two groupings of individuals with almost nonoverlapping sizes, early and lately maturing, and the latter group inhabits, in the mean, more southern and warmer areas, than the former. But the ranges of these two groupings widely overlap within the area studied. In this respect *G. borealis* is similar to such species of oceanic ommastrephids as *Sthenoteuthis pteropus, Ommastrephes bartramii, Dosidicus gigas.* We have no data, whether these two groupings of *G. borealis* have different spawning time, as spawning in this species is very protracted, and in the NE Pacific it reproduces all the year round (Kubodera et al. 1983, Kubodera and Jefferts 1984), and we cannot distinguish early and lately maturing squids at I stage of maturity.

An important distinction between *G. borealis* and oceanic ommastrephids is that the lately maturing groupings in the former species inhabit in the average more warm area than the early maturing grouping, while in oceanic ommastrephids the opposite is true (Nesis 1983, 1993, Zuev et al. 1985). The association of lately maturing grouping in *G. borealis* with relatively warm water along the northern periphery of Kuroshio Current and North Pacific Drift (Kubodera et al. 1983) is an unique feature of this species and contradicts the rule for squids: in warmer waters the squids mature faster than in colder and complete their life cycle at smaller size (Mangold 1987).

The status of two groupings in *G. borealis* remains unclear. We can see that among the males the lately maturing group is represented by adult specimens only and the group of immature specimens is not subdivided into the early and the lately maturing subgroups. Thus, judging by males only, it may be concluded that the larger males survive after their first spawning season, i.e. they are the small-sized males which do not die after the first season of mating and live for the next year. The supposition about the possibility of surviving of males during two subsequent reproductive seasons was repeatedly expressed for small number of species of loliginid squids and octopodid octopuses, in which the males mature, as usual, much earlier than females, but the largest specimens are invariably males (Hixon et al. 1981, Mangold 1983, 1987, Summers 1983, etc.).

This supposition however should be rejected for *G.borealis* because, firstly, the curves approximating the penis growth cross the X-axis at different size: 10-11 cm in early maturing and 16-17 cm in lately maturing males and, secondly, all largest males in both our and Japanese collections (Kubodera et al. 1983, Naito et al. 1977b) are noticeably smaller than largest females (as it is usual for squids).

If our supposition is true that the females with size characteristic of early maturing grouping, but with nidamental glands smaller than in most females at respective maturity stage, are in fact immature and maturing females of the lately maturing grouping, it is necessary to make the conclusion: the differences between early and lately maturing squids, at least in females, are formed well before the final stages of maturation and may be genetically determined. In this case we may say that early maturing and lately maturing groupings are really different stock units, or units of suprapopulational rank. The supposition (Nesis 1989) about one-year life cycle in early maturing and two-year — in lately maturing squids remains a hypothesis.

B. magister. Our data are so scanty that it is impossible to make any somewhat grounded conclusion. We may only say that, firstly, in *B. magister* the early and lately maturing groups may exist too and, secondly, that lately maturing squids absolutely predominate throughout the species range. Early maturing squids may appear only in times of strong decline in abundance of common, lately maturing grouping.

If the above-said is true, then intraspecific structure of *B. magister* is different from that in *G. borealis* and similar only to the structure of tropical Indo-Pacific ommastrephid *Sthenoteuthis oualaniensis*. In the latter species, together with common and widely distributed middle-sized and local (Arabian Sea) giant forms, a dwarf early maturing form exists, which is so distinct that there were many attempts to describe it as a separate species (see reviews: Nesis 1985, 1993, Zuev et al. 1985). The important difference is that the dwarf form of *S. oualaniensis,* partially sympatric with the common (middle-sized) form, exists constantly and has wide range located in central part of the range of the common form. It is possible to find another analogy for *B. magister* in the nerito-oceanic ommastrephid squid *Todarodes pacificus*, which also has a dwarf form — a separate subspecies *T. pacificus pusillus* (Dunning 1988). But this dwarf form is fully allopatric in relation to the nominotypical subspecies and inhabits much warmer equatorial waters.

The data presented contradict the R.K. O'Dor's (1992) supposition that in the areas influenced by western boundary currents after the catastrophic decline in abundance of large populations of large-sized squids, caused by physical events, these populations are probably «re-evolved» from more stable tropical/subtropical populations of small squids of the same species. This hypothesis seems applicable to nerito-oceanic ommastrephids but not to gonatids.

In general, our data show that the phenomenon of intraspecific groupings is peculiar not only for the families Loliginidae (where it is characteristic of only some species) and Ommastrephidae (where it is peculiar for most species), but for the family Gonatidae too. It may be supposed that this biological feature has evolved independently in various squids as well as in various groups of fishes and fish-like animals (cyclostomes) as an adaptation to subdivision of species ecological niches and to diminishing the intraspecific competition in abundant and prosperous species of active animals.

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Внутривидовые группировки у кальмаров-гонатид

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РЕЗЮМЕ. В ловах из эпипелагиали (0-50 м) южной части Охотского моря и прикурильских вод Тихого океана (118 часовых тралений крупногабаритными разноглубинными оттер-тралами) и мезопелагиали (500-300-200 м) до 200 миль к востоку — юго- востоку от южных Курильских островов (11 тралений) в июле-августе 1992 г. кальмар *Gonatopsis borealis* занимал 1-2 места по численности и биомассе среди всех кальмаров и был представлен двумя внутривидовыми группировками — мелкой раннеспелой (МГ) и крупной позднеспелой (КГ). МГ распространена по всему району исследований, КГ только к востоку и юго-востоку от южных Курил вдали от берегов. Модальная длина мантии (ДМ) у зрелых самцов и созревающих самок МГ 12-17 и 13-17 см, КГ — 20-26 и 22-27 см. В эпипелагиали Охотского моря созревающих кальмаров очень мало, зрелых самцов нет, в Тихом океане созревающие самцы и зрелые самки встречены как в эпи-, так и в мезопелагиали, но ни одной зрелой спаривавшейся самки не было добыто. Рост пениса у самцов начинается при ДМ 10-11 см (переход из I во II стадию зрелости) и резко замедляется при ДМ 19-20 см. Самцы КГ представлены только зрелыми особями, неполовозрелые самцы не разделяются на МГ и КГ. Рост нидаментальных желез у самок МГ и КГ происходит ускоренно и приблизительно параллельно. Имеется небольшое число самок с размером, типичным для МГ, но с менее развитыми, чем у основной массы самок, нидаментальными железами; возможно, это — самки КГ. Если это так, различия между самками МГ и КГ закладываются задолго до созревания. Гонадосоматический индекс у самцов КГ немного выше, а у самок немного ниже, чем у МГ на той же стадии зрелости. Командорский кальмар *Berryteuthis magister* был крайне малочислен и в Охотском море, и в прикурильских водах Тихого океана (0.16 и 0.04% общей биомассы кальмаров). Кроме единичных особей обычных размеров, у восточного Сахалина над глубинами 92-320 м добыто 2 самца на II и III стадиях и 4 самки на II стадии зрелости необычно малых размеров — ДМ 6-10 см (обычно переход из I во II стадию происходит при ДМ 14-18 см). Возможно, это — особи из не известной ранее скороспелой группировки, быть может, появляющейся лишь в периоды резкого снижения численности обычной группировки. Обсуждается статус МГ и КГ у гонатид в сравнении с лолигинидами и оммастрефидами.